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Soil C and N pools in patchy shrublands of the Negev and Chihuahuan Deserts

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Abstract

Patchy distribution of vegetation within semi-arid shrublands is normally mirrored in the soil beneath perennial shrubs (macrophytic patches), compared to inter-shrub areas (microphytic patches). To determine impacts of (1) litterfall inputs within vegetation patches and (2) rainfall distribution on soil C and N, we investigated soil C and N pools and associated soil properties in two semi-arid shrublands, in the Negev Desert of Israel (Lehavim), which receives >90% of annual rainfall during winter and in the Chihuahuan Desert, USA (FHMR) that experiences a bimodal (Summer–Winter) annual rainfall pattern. We also evaluated grazing effects on soil C and N pools at Lehavim. More distinct differences in soil properties existed between patch types at the Negev site, where the soils contained higher soil organic C and N, amino acids and sugars, asparaginase activity and plant-available N than those at FHMR. Soil organic C (0–5 cm) in macrophytic patches was 39 g/kg at Lehavim and 13 g/kg at FHMR, and asparaginase activity was as high as 70 μg N/g 2 h in macrophytic patches at Lehavim, two times higher than at FHMR. The soil (0–5 cm) $\delta^{13}C$ was −15 to −18‰ at Lehavim and −18 to −19‰ at FHMR, with significantly lower $\delta^{13}C$ in macrophytic patches at both sites. The $\delta^{13}C$ suggested that considerable macrophytic patch soil C was derived from cyanobacteria at Lehavim and C4 grasses at FHMR. Plant litter $\delta^{15}N$ was 0.9‰ at Lehavim and 0.6‰ at FHMR, suggesting that much plant N was derived from N fixation. Concentrations of inorganic soil N ($NH_4^+ + NO_3^-$) were up to 37 mg N/kg at Lehavim and <9 mg N/kg at FHMR. Grazing at Lehavim resulted in lower soil CH, AA, and AS. We conclude that differences between the sites are due largely to (i) higher amounts of litterfall C and N inputs within macrophytic patches at Lehavim and (ii) the different precipitation patterns, with summer precipitation at FHMR promoting increased organic matter mineralization compared to Lehavim, which experiences Winter precipitation only. Furthermore, greater differences in soil properties between patch types at Lehavim compared to FHMR can likely be attributed to the increasing importance of physical processes of resource dispersion at the more humid site in Arizona.

Keywords: Fertile islands; Soil nutrient pools; Carbohydrates; Amino sugars; Amino acids; Fertile islands; Enzyme activity

1. Introduction

Vegetation distribution within arid and semi-arid shrublands is often described as "patchy", with macrophytic patches dominated by one or more woody perennial plants, and microphytic patches the domain of ephemeral plants and biological soil crusts. Within such ecosystems "fertile islands" are usually centered in macrophytic patches, and the soils beneath tend to be enriched with C, N and P, compared to microphytic patches (Schlesinger et al., 1990; Whitford, 2002). The macrophytic patches also tend to be enriched in microbial activity and diversity and enzyme activity compared to microphytic patches (Herman et al., 1995; Zaady et al., 1996).

Abbreviations: CH; Carbohydrates; AA; Amino acids; AS; Amino sugars

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Vegetation distribution within the semi-arid northern and northeastern Negev Desert region of Israel is a mosaic of macrophytic patches dominated by shrubs such as *Sarcopoterium spinosum* and C3 annual grasses, and microphytic patches featuring mostly grasses and a biological soil crust dominated by algae, cyanobacteria, lichens and mosses (Shem-Tov et al., 1999; Ungar et al., 1999; Zaady et al., 1994, 1996). Shrubs common to the area, including *S. spinosum*, are incapable of N-fixation. However, they host a community of non-symbiotic N fixers whose activity provides a substantial portion of the plant N requirement. In addition, cyanobacteria fix N in microphytic patches, and this N may subsequently be transported by overland flow of water to macrophytic patches (Zaady et al., 1998).

The semi-arid northern Chihuahuan Desert of southeastern Arizona, USA, with a bimodal precipitation pattern, can also be described as a patchy landscape, with the leguminous shrub or tree *Prosopis velutina* dominating the macrophytic patches, and perennial and annual C3 and C4 grasses and soil crusts dominating microphytic patches. Symbiotic N fixation and subsequent decomposition of litterfall from *P. velutina* is a major source of soil N in this landscape. Their senesced leaves may contain up to 3.5% N (Killingbeck and Whitford, 1996; Wilson and Thompson, 2005).

Increasing predominance of woody species has been observed in arid and semi-arid regions across the world. Human influence is often implicated in these vegetation changes (Whitford, 2002). Altered climatic conditions (Polley et al., 1994) and land use by man (Brown and Archer, 1989) are the main factors that have influenced the spread of *Prosopis* spp. within the past several decades from historic drainage locations to more xeric open areas in the southwestern USA (Wilson et al., 2001). This has resulted in a corresponding alteration of soil nutrient distribution as mesquite becomes a major component of the plant biomass of desert grasslands (Tiedemann and Klemmedson, 1977; Wilson and Thompson, 2005). Woody plant abundance has also been linked to an increase in C and N sequestration in these semiarid ecosystems (Schlesinger et al., 1990; Hibbard et al., 2001). *Sarcopoterium* has similarly spread in the northern Negev Desert in Israel, as thousands of years of livestock grazing (Perevolotsky, 1999) have affected the plant community structure throughout much of the hilly semiarid rangelands.

Heterogenous soil nutrient pools, associated with the "fertile island" phenomenon, affect nutrient conservation and storage within ecosystems, and have direct effects on organic matter mineralization dynamics, a key component of C and N cycling. Soil enzyme activities have been previously used as indicators of soil C and N mineralization dynamics. For example, Blank (2002) noted significantly higher activities of N-mineralizing enzymes at microsites under plant canopies than in open areas in a Great Basin sagebrush ecosystem; this activity decreased with increasing soil depth, and was directly correlated with soil N concentrations. Mineralization dynamics can also be evaluated by measurements of available soil N through time and space. For example, Schlesinger et al. (1996) reported that in arid Chihuahuan Desert shrublands, soil NO_3^- followed closely the distribution of *Larrea tridentata* shrubs. Kieft et al. (1998) observed that soil NO_3^- in Chihuahuan Desert shrublands varied more through time than in adjacent grassland. Wilson and Thompson (2005) found that in a semi-arid Chihuahuan Desert shrubland, spatial patterns of soil NO_3^- were stable with time and corresponded closely to the distribution of *P. velutina*.

In this study we evaluated impacts of litterfall inputs within macrophytic patches and rainfall distribution on soil C and N in these two semi-arid ecosystems. Understanding soil C and N storage and potential responses of nutrient pools within these landscapes to disturbance will result in better management options for grazing or C management. Vegetation and nutrient distributions within Negev and Chihuahuan shrublands are expected to exhibit patchiness. However, these landscapes differ in macrophyte type (non-legume in the Negev, legume in the Chihuahuan), size (<1 m tall in the Negev, up to 4 m tall in the Chihuahuan), average annual rainfall (275 mm in the Negev, 380 mm in the Chihuahuan), and rainfall distribution. We predict that (1) differences in litterfall C and N in macrophytic patches and differences in rainfall distribution will result in differences in macrophytic patch soil C and N between these sites and (2) more distinct differences in soil nutrient pools between patch types should exist at the more arid site. Grazing was a part of the treatment structure at Lehavim, and we predicted that grazing will change resource inputs and thus, nutrient pools. Our objectives were to evaluate within macrophytic and microphytic patch types in semi-arid Negev and Chihuahuan shrublands: (1) soil organic C and N, C and N isotope ratios, soil carbohydrates, amino acids and sugars, asparaginase activity and glucosamine:galactosamine ratios; (2) seasonal variation in plant available N and P; and (3) the relationship between litterfall C and N returned to the soil and these soil properties.

2. Materials and methods

2.1. Site description

Study sites were established in semi-arid shrublands in Israel and Arizona for soil and litterfall sampling. The site in Israel was located at the Lehavim Long-Term Ecological Research (LTER) station in the northern Negev Desert. The Lehavim station is located 15 km North of Beer Sheva (latitude 31°22′N, longitude 34°50′E, elevation 350–450 m). The mean annual rainfall of 275 mm occurs almost entirely during November through March. The mean summer temperature is 25 °C and the mean winter temperature is 10 °C (Osem et al., 1999). The vegetation at Lehavim has a patchy distribution, with C3 *S. spinosum* shrubs (<1 m in height) and C3 annual grasses dominating macrophytic patches 1–3 m in diameter, and biological soil crusts and C3 annual grasses and forbs dominating the intervening microphytic patches (Zaady et al., 1994). Plots were located in adjacent ungrazed areas and areas with controlled grazing by sheep and goats, where grazing was controlled by fencing. This area of the Negev has been grazed for centuries; "ungrazed" denotes grazing exclusion for the previous 2 yr. Grazing occurred within enclosures (2000 m^2) in the grazed plots twice: in January and May. At each time, 190 to 200 sheep and goats were allowed in the plots for 30–45 min.

The site in Arizona was located in northern Chihuahuan semi-arid shrublands on the US Army's Ft. Huachuca Military Reservation (FHMR) near Sierra Vista, Arizona, USA (latitude: 31°33′N, longitude: 110°18′W, elevation 1490 m). The mean annual rainfall of 380 mm is distributed almost equally between a winter rainy season (November–March) and a Summer monsoon season (July–September). The mean Summer and Winter temperatures are 25 and 9.5 °C, respectively (WRCC, 2005). Similar to Lehavim, at FHMR vegetation has a patchy distribution, with the legume *P. velutina* dominating macrophytic patches 1–6 m in diameter. Intervening microphytic patches are dominated by soil crusts, and C3 and C4 annual and perennial grasses and forbs (Wilson and Thompson, 2005). No livestock grazing has been allowed at FHMR since the 1940s, and no fires have been recorded since 1949.

2.2. Plant and soil sampling

Ten *P. velutina* were selected for litterfall sampling at FHMR, and ten *S. spinosum* were selected at Lehavim. At FHMR, 20 L plastic buckets were used as traps, positioned around the base of each shrub in two rings of five traps each. Traps were located on N, S, E, W and NE axes; the inner ring was placed at a distance of one-half the canopy radius from the center of the shrub, and the outer ring was positioned at the canopy edge. At Lehavim, 1 L traps were placed so that the top of each trap was 23 mm above the soil surface, with eight traps positioned around the base of each shrub patch in two rings of four traps each. Traps were located on N, S, E and W axes; the inner ring was placed at a distance of one-half the canopy radius from the center of the shrub, and the outer ring was positioned 0.5 m outside the canopy edge. Litterfall was collected monthly for 12 months, dried for 6 h at 60 °C, and weighed after extraneous matter (e.g. insects) was separated from plant litter. During some months, no litterfall was found. Three monthly samples were composited to form one sample per shrub for chemical analyses. After drying, samples were ground to pass a 100-mesh sieve, and organic C, organic N, $\delta^{13}C$ and $\delta^{15}N$ were determined in selected samples as described below.

Five additional *P. velutina* were selected for soil sampling at FHMR. Samples were collected along cardinal direction axes centered on the central axis of the shrub, inside the macrophytic patch at one-half the canopy radius and within microphytic patches at 1.5 times the canopy radius. O horizon material, where it occurred, was collected separately, and samples of mineral soil were collected from 0–5 and 5–10 cm increments. Sampling dates were 1 November 2001, and 10 February, 16 May and 19 August 2002. At Lehavim, five *S. spinosum* in the ungrazed area, and five in the grazed area, were selected for soil sampling. Samples of mineral soil (no O horizon was present) were collected from the 0–5 cm depth along the four cardinal directions, inside and outside (0.5 m) the canopy of *S. spinosum* on 4 October 2001 and 15 April 2002. Soil samples were dried and ground to < 2 mm for NH_4^+ and NO_3^- analysis. Samples were ground to pass a 100-mesh sieve for the other analyses discussed below.

2.3. Soil, plant and data analyses

Soil samples from both experimental sites were analyzed as follows. Organic C and total N contents were determined using an on-line elemental analyzer (PDZ Europa ANCA-GSL) after sample combustion to CO_2 and N_2 at 1000 °C, and $\delta^{13}C$ and $\delta^{15}N$ were measured by continuous flow isotope ratio mass spectrometry (20–20 mass spectrometer, PDZ Europa, Northwich, UK). Sample isotope ratios were compared to those of standards ($\delta^{13}C$ of Pee Dee Belemnite and $\delta^{15}N$ of air). Samples from Lehavim contained free $CaCO_3$, and were treated by acid fumigation with HCl (Harris et al., 2001) to remove inorganic C before analysis. Soils from FHMR had pH $\leqslant$ 6, and did not contain free $CaCO_3$. Therefore they were not acid-treated prior to C and N analysis. Phosphorus extractable with $NaHCO_3$ (Kuo, 1996) was determined in soil samples from one season. Nitrogen ($NH_4^+ + NO_3^-$) extractable with 2 M KCl (Keeney and Nelson, 1982) was measured in all soil samples by using colorimetric analysis. Activity of L-asparaginase was measured on all 0–5 cm soil samples collected on 16 May 2002 at FHMR and 15 April 2002 at Lehavim by measuring amounts of NH_4^+ released during soil incubation for 2 h at 37 °C in the presence of *tris*-hydroxy-aminomethane (THAM) and L-asparagine (Tabatabai, 1994). In selected soil samples, CH (carbohydrates) were extracted with 12 M H_2SO_4 for 30 min followed by a 30 min autoclave hydrolysis with 1.5 M H_2SO_4 at 121 °C, and quantified using ion chromatography following Martens and Loeffelmann (2002). In selected soil samples, AA (amino acids) and AS (amino sugars) were hydrolyzed with 4 M methanesulfonic acid for 1 h at 136 °C and 112 kPa in an autoclave, and the released AA and sugars were quantified by ion chromatography with pulsed amperometric detection (Martens and Loeffelmann, 2003). Total C, total N, $\delta^{13}C$ and $\delta^{15}N$ were analyzed in litterfall samples as discussed above.

Analysis of variance was performed within each site by using the GLM procedure of SAS (SAS Institute, 2000). Experiments at Lehavim were conducted in separate but adjacent blocks with and without grazing. Analysis of variance across blocks was conducted after first verifying equality of variance (grazed vs. ungrazed) using the chi-square test described by Gomez and Gomez (1984). The general form of the ANOVA model used included the main effects of grazing, direction, and patch type, and all interaction terms. Nonsignificant terms were dropped from the models and reduced models were run again. At FHMR, the general form of the ANOVA models included the main effects of direction and patch type and interactions. Comparisons of measured soil properties between sites were performed by using a student's *t*-test.

3. Results

3.1. Lehavim

Most litterfall occurred during November–May. During the period of litter collection (September 2001–August 2002), rainfall was 195 mm, compared to the long-term average of 275 mm. Litterfall C within grazed macrophytic patches was 258 g/m^2 yr (S.D. = 25, $n = 10$), while litterfall C in ungrazed macrophytic patches was 164 g/m^2 yr (S.D. = 13, $n = 10$). Nitrogen in litterfall was 7.9 g/m^2 yr (S.D. = 0.8, $n = 10$) in grazed plots and 4.6 g/m^2 yr (S.D. = 0.4, $n = 10$) in ungrazed plots.

Soil organic C (SOC) concentrations were approximately 25% higher within macrophytic patches compared to microphytic patches (Table 1; Fig. 1(A)). Soil $\delta^{13}C$ was about 2‰ lower in macrophytic patches, and were significantly affected by grazing treatment (Table 1, Fig. 2(A)). Soil organic N (SON) concentrations (Fig. 1(B)) followed similar trends as SOC, with significantly higher concentrations within macrophytic patches. However, differences between patch types were higher than for SOC. In plots without grazing, mean soil C:N from both patch types was 12.6, while in plots with grazing, mean C:N ratio was 14.4. The soil $\delta^{15}N$ within macrophytic patches was $\geqslant 1.5$‰ lower ($p < 0.05$) than that in microphytic patches (Fig. 2(B)).

Both grazing and patch type significantly affected soil CH concentrations (Table 1, Fig. 3(A)). In all cases glucose and galactose were the major CH recovered (Table 2). Total CH were linearly correlated ($r^2 = 0.58$, $p < 0.01$) with organic C, and about 10% of SOC was recovered as CH–C. Grazing resulted in significantly lower CH (Table 1, Fig. 3(A)) and lower soil AA and AS (Table 1, Fig. 3(B)), with highest values found in macrophytic patches. In all cases, the major AA were arginine and aspartic acid, and the major AS was glucosamine (Table 3). Total AA and AS were correlated ($r^2 = 0.79$, $p < 0.01$) with organic N, and 49% of SON was recovered as AA and AS. Similar to the CH, we note that grazing resulted in lower concentrations of AA and AS in soils, thus a smaller pool of labile soil N, without resulting in significantly lower SON.

Asparaginase activity is an index of heterotrophic microbial populations and relative soil N-mineralization potential. Asparaginase activity was significantly ($p < 0.05$) higher ($> 2\times$) within macrophytic patches, but was not significantly affected by grazing (Table 1, Fig. 3(C)). Asparaginase activity was not significantly correlated ($p = 0.05$) with either organic C or available N.

Soil inorganic N ($NH_4^+ + NO_3^-$) concentrations measured in October were significantly higher within macrophytic than microphytic patches (Table 1, Fig. 4(A)). These samples were collected after 6 months without rainfall, therefore these concentrations likely represent N mineralized during the previous rainy season that was not taken up by plants nor lost through other mechanisms. In October, 44% (S.D. = 9) of inorganic N was NO_3^-, with the rest found as NH_4^+ (data not shown). Both grazing and patch type significantly affected inorganic N concentrations during October. Samples collected in April following the winter rainy season (255 mm of rainfall October and April) had lower inorganic N concentrations and indicate that conditions during this period were conducive to N uptake by plants and (or) N losses, compared to N mineralization. An average of 37% of inorganic N (S.D. = 13) was found as NO_3^- in April. In the April sampling there were no significant differences in inorganic N between patch types, but there was significantly ($p < 0.05$) higher inorganic N in grazed plots (Table 1). Extractable P was measured only once because, in contrast to inorganic N, temporal concentration differences were expected to be low. Similar to inorganic N, extractable P was significantly ($p < 0.05$) higher within macrophytic patches (Table 1, Fig. 4(B)), and with grazing.

Table 1
Analysis of variance summary for soil properties measured at Lehavim

Source	Organic C	Organic N	$\delta^{13}C$	$\delta^{15}N$	Inorg N Date 1	Inorg N Date 2	Soil Ext. P Date 1	Total carbs	Total aminos	Asparaginase activity
Grazing	NS	NS	**	NS	*	**	**	*	*	NS
Patch type	**	**	**	**	**	NS	**	**	**	**
Direction	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Direction × Patch type	*	NS	**	NS	NS	NS	NS	**	NS	NS

*,** Significant at $p = 0.05$ and 0.01, respectively.
NS—not significant ($p > 0.05$).

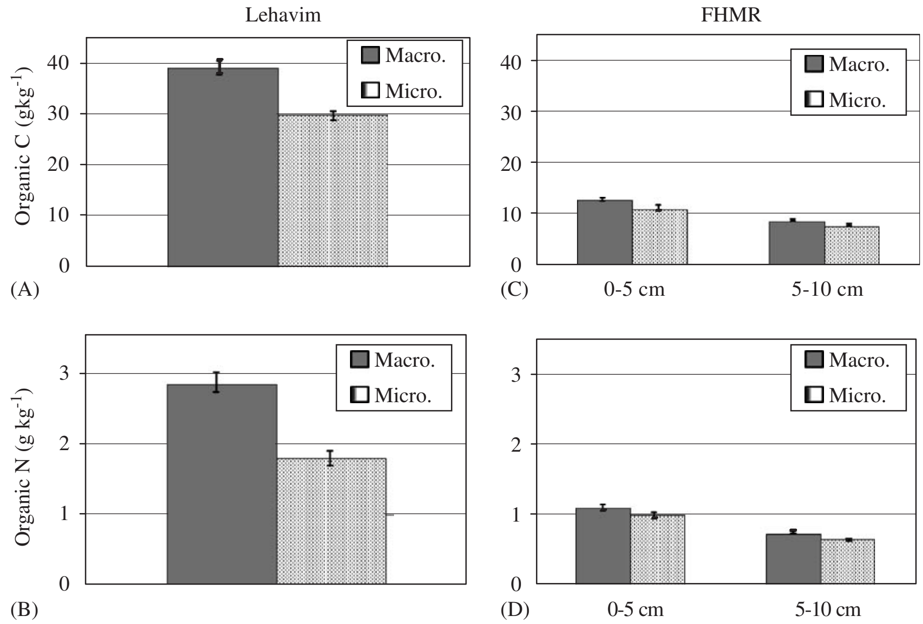

Fig. 1. Soil organic C (A) and organic N (B) from 0–5 cm at Lehavim, and organic C (C) and organic N (D) from 0–5 and 5–10 cm at FHMR. At Lehavim, values are averages across grazing treatments. Error bars indicate standard error of the mean.

Table 2
Major carbohydrate profile for 0–5 cm soil samples at Lehavim and FHMR

Location	Grazing	Patch type	Carbohydrate concentrations (g/kg)						
			Arab[a]	Rham	Gal	Gluc	Xyl	Man	Total
Lehavim	None	Macro.	1.63a[b]	0.81a	2.06a	2.37a	1.04a	1.22a	10.1a
		Micro.	0.97b	0.46b	1.11c	1.14b	0.52b	0.67b	6.9b
	With	Macro.	1.42a	0.57b	1.41b	2.02a	0.86a	1.06a	7.3b
		Micro.	0.98b	0.34c	0.92c	1.26b	0.55b	0.70b	5.0c
FHMR	NA	Macro.	1.56a	0.33a	1.33a	1.89a	1.53a	0.78a	7.4a
		Micro.	1.08a	0.35a	1.11a	1.81a	1.16a	0.63a	6.1a

[a]Abbreviations: Arab, arabinose; Rham, rhamnose; Gal, galactose; Gluc, glucose; Xyl, xylose; Man, mannose.
[b]Numbers within a location and column followed by the same letter are not significantly different at $p = 0.05$.

3.2. FHMR

At FHMR, litterfall was also collected during a 1 yr period, and most litterfall occurred during June–December. During the period of litter collection (October 2001–October 2002), rainfall was 249 mm, compared to the long-term average of 380 mm. Carbon contained in litterfall under the shrubs was 47.2 g/m^2 yr ($n = 20$, S.D. = 17.0), and N was 2.6 g/m^2 yr ($n = 20$, S.D. = 0.9). Both C and N deposited in litterfall were much lower than at Lehavim.

Soil organic C and N concentrations (Figs. 1(C) and 1(D)) were both significantly ($p < 0.05$) higher within macrophytic than microphytic patches, at both the 0–5 and 5–10 cm depths (Table 4). In contrast to Lehavim, soil C:N ratio was identical within both patch types (11.1, S.D. = 0.1) at the 0–5 cm depth. The δ^{13}C was −16 to −19‰ (Fig. 2(A)), with significant differences ($p < 0.05$) between patch types at both depths (Table 4). The δ^{15}N was 4.9 to 5.9‰ (Fig. 2(B)) and values were significantly ($p < 0.05$) different between patch types at 0–5 cm.

Carbohydrate, AA, and AS concentrations were different among depths, with concentrations of both more than 30% higher within the 0–5 cm depth (Figs. 3(D) and 3(E)). Unlike Lehavim, O horizons were found under most shrubs at Ft. Huachuca. Carbohydrate concentrations in the O horizons were similar to those in the 0–5 cm depth (8.0 g/kg, S.D. = 3.1), while AA and AS concentrations in O horizons were much higher (19.3 g/kg, S.D. = 6.0, data not shown) than at 0–5 cm. Within both patch types, glucose was the CH present in the highest concentrations (Table 2), although there were no significant differences in total (Table 4) or individual (Table 2) CH concentrations between patch types. Similar to Lehavim, about 10% of

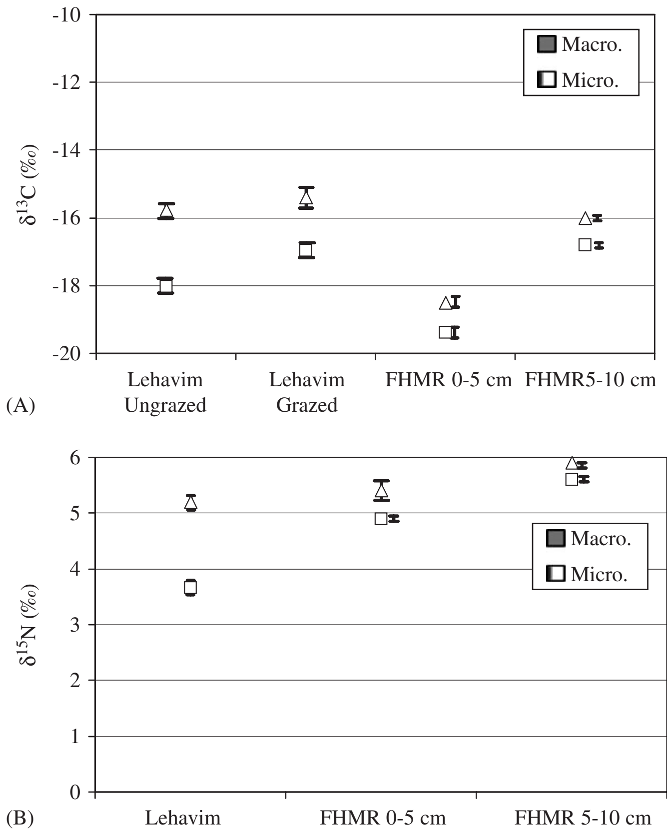

Fig. 2. Soil δ^{13}C from 0–5 cm at Lehavim and 0–10 cm at FHMR (A), and soil δ^{15}N from 0–5 cm at Lehavim and 0–10 cm at FHMR. Error bars indicate standard error of the mean.

soil C in the 0–5 cm depth was identifiable as CH. A majority (60%) of soil N was recovered as AA and AS. Amino acids and sugars were related in a linear fashion to organic N ($r^2 = 0.70$). Similar to CH, there were no significant differences in individual AA or AS concentrations between patch types (Table 3). Arginine, aspartic acid and glutamic acid were the most common AA, and glucosamine was the most common AS. The AA and AS concentrations in soils of both patch types were significantly higher at Lehavim than at FHMR (Table 5). However, the amino acid profiles were similar (Table 3). Arginine was the most common AA, comprising 10–13% of SON.

Asparaginase activity was two-fold higher in the 0–5 cm depth compared to the 5–10 cm depth. However, there were no differences between patch types (Fig. 3(F), Table 4). Within O horizon material, asparaginase activity averaged 82 μg N/g 2 h ($n = 19$, S.D. = 12), much higher than in mineral soil.

Soil inorganic N concentrations (Fig. 4(C)) followed similar trends in both depth increments, but were usually two times higher at 0–5 cm (data not shown for 5–10 cm depth). Concentrations were highest during November, at the beginning of the Winter rainy season. Concentrations were progressively lower at the next two sampling dates,

Table 3
Major amino acid and amino sugar profile for 0–5 cm soil samples at Lehavim and FHMR

Location	Grazing	Patch type	Concentrations of amino acids and sugars (g/kg) Arg[a]	Orn	Lys	Gal	Gluc	Ala	Thr	Gly	Val	Ser	Pro	Leu	Glut	Asp
Lehavim	None	Macro.	1.21a[b]	0.16a	0.62a	0.38a	0.95a	0.68a	0.48a	0.78a	0.49a	0.48a	0.44a	0.43a	0.82a	0.88a
		Micro.	0.77b	0.11b	0.41b	0.19b	0.51b	0.41b	0.25b	0.51b	0.27b	0.26c	0.25b	0.22b	0.52b	0.69b
	With	Macro.	0.95a	0.15a	0.50a	0.31a	0.73a	0.52a	0.46a	0.60a	0.37a	0.37b	0.35a	0.28b	0.51b	0.68b
		Micro.	0.58b	0.12b	0.36b	0.19b	0.49b	0.37b	0.30b	0.44b	0.25b	0.24c	0.24b	0.18c	0.34c	0.55c
FHMR	NA	Macro.	0.52a	ID	0.28a	0.19a	0.37a	0.24a	0.17a	0.37a	0.15a	ID	ID	0.18a	0.39a	0.37a
		Micro.	0.53a	ID	0.27a	0.16a	0.31a	0.22a	0.16a	0.34a	0.14a	ID	ID	0.16a	0.42a	0.37a

ID signifies insufficient data to calculate means.
[a]Abbreviations: Arg, arginine; Orn, ornithine; Lys, lysine; Gal, galactosamine; Gluc, glucosamine; Ala, alanine; Thr, threonine; Gly, glycine; Val, valine; Ser, serine; Pro, proline; Leu, leucasine; Glut, glutamic acid; Asp, aspartic acid.
[b]Numbers within a location and column followed by the same letter are not significantly different at $p = 0.05$.

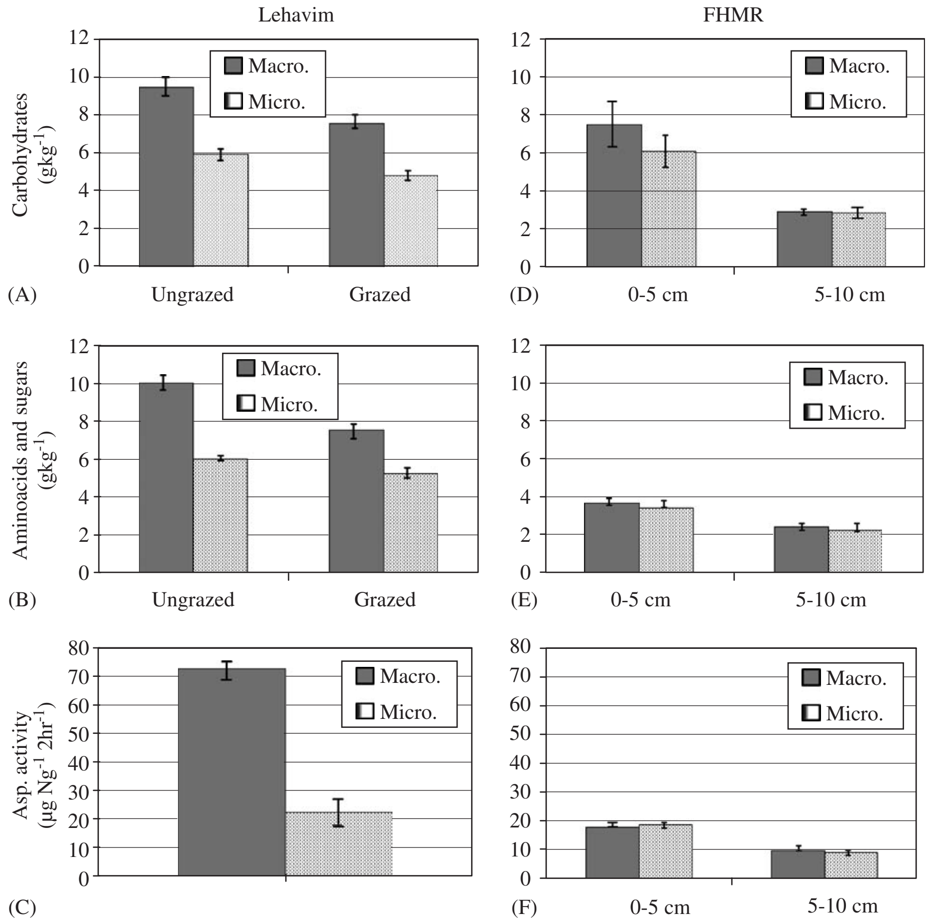

Fig. 3. Soil (0–5 cm) hydrolysable carbohydrates (A), amino acids and sugars (B), and asparaginase activity (C) at Lehavim; and soil (0–10 cm) hydrolysable carbohydrates (D), amino acids and sugars (E) and asparaginase activity (F) at FHMR. Values for asparaginase activity at Lehavim are averages across grazing treatments. Error bars indicate standard error of the mean.

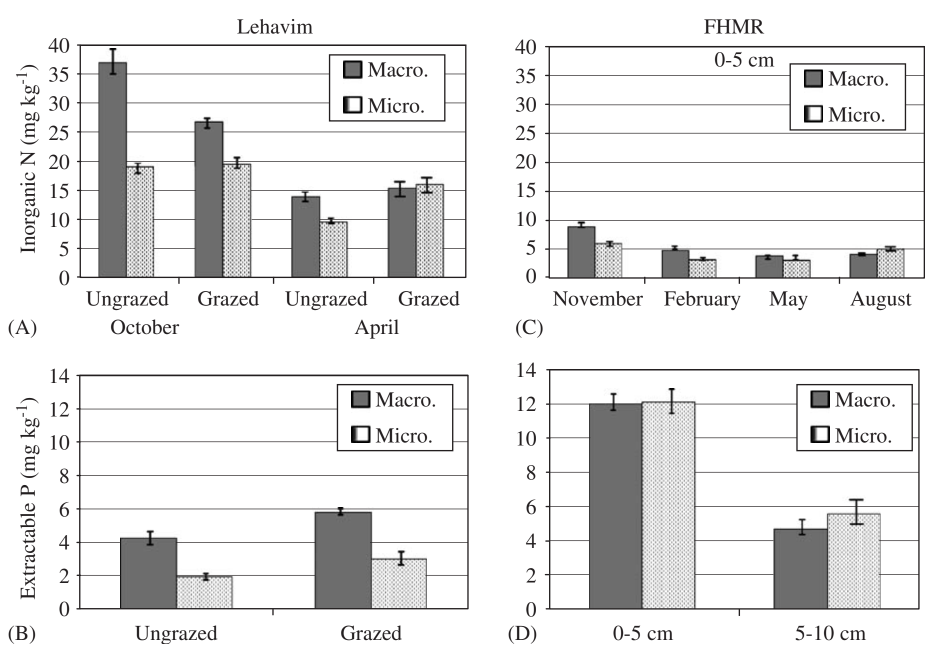

Fig. 4. Soil (0–5 cm) inorganic N ($NH_4^+ + NO_3^-$) (A) and bicarbonate extractable P (B) at Lehavim and soil inorganic N (C) and bicarbonate-extractable P (D) at FHMR. Error bars indicate standard error of the mean.

Table 4
Analysis of variance summary for soil properties measured at FHMR

Source	Organic C	Organic N	δ^{13}C	δ^{15}N	Inorganic N				Inorg. P	Total carbs.	Total aminos	Asparag. activity
					Nov.	Feb.	May	Aug.				
0–5 cm depth												
Patch type	**	**	*	*	*	*	NS	NS	NS	NS	NS	NS
direction	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Patch type × direction	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS
5–10 cm depth												
Patch type	*	*	*	NS	NS	*	NS	NS	NS	NS	NS	NS
direction	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Patch type × direction	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

*,** Significant at $p = 0.05$ and 0.01, respectively.
NS—not significant ($p > 0.05$).

Table 5
Summary of students *t*-test comparisons of measured soil properties between macrophytic and microphytic patches at the Lehavim and FHMR experimental sites

Soil property	Patch type	
	Macrophytic	Microphytic
Organic C	***	***
Organic N	***	***
C:N ratio	**	***
δ^{13}C	**	***
δ^{15}N	***	NS
Asparaginase activity	***	NS
Total AA and AS	***	***
Total CH	NS	NS
Glucosamine/galactosamine ratio	***	***

Comparisons were performed for the 0–5 cm depth in ungrazed plots only.
*,**, *** Signifies significant differences within patch types between sites at $p = 0.05$, 0.01 and 0.001, respectively.
NS—not significant ($p > 0.05$).

and rose again at the final sampling in August, during the Summer monsoon season. Differences in concentrations between patch types were significant for the first two sampling dates (Table 4). A maximum of 79% (S.D. = 11) of available N was found as NO_3^- in November, following the Summer monsoon season, while only 38% (S.D. = 18) was NO_3^- in February, following the Winter rainy season. Concentrations of extractable P at 0–5 cm were more than twice those at Lehavim, with no significant differences in soil P between patch types. Similar to inorganic N, higher concentrations of P near the soil surface suggest limited downward movement of P (Fig. 4(D)).

4. Discussion

The distributions of soil C, N, and P at both sites were consistent with earlier descriptions of "fertile islands" in arid and semi-arid ecosystems (e.g. Schlesinger et al., 1990; Whitford, 2002), with higher concentrations of organic C and N, inorganic N and P, and enzyme activity within macrophytic patches. In general, nutrients followed similar distributions between patch types at both sites. Therefore, superficially the nutrient pools and distributions at these sites appear similar. Upon closer examination, however, some striking differences emerge between the sites.

4.1. Soil organic C and N

Soil organic C and SON concentrations (0–5 cm depth) were about three times higher at Lehavim than at FHMR, within both patch types, and these differences were significantly different (Table 5). Soil C and N concentrations that we observed at Lehavim are consistent with earlier reports. Zaady et al. (2001b) found up to 6% SOM (SOC of approximately 19 g/kg) at 5–10 cm within macrophytic patches at Sayeret Shaked in the Negev, which receives less rainfall than Lehavim. He et al. (2002) reported up to 58 g SOC/kg at 0–10 cm within macrophytic patches at a Negev site receiving 90 mm of annual rainfall. Our soil C and N concentrations are also consistent with those previously reported for Chihuahuan Desert soils. For example, Tiedemann and Klemmedson (1986) reported that SOC (0–4.5 cm) under *Prosopis* was 8.0 g/kg at a site in southern Arizona with 330 mm annual rainfall. These findings suggest higher rates of C and N storage at shallow depths in soils of the Negev compared with those from the wetter Chihuahuan semi-arid grass and shrublands.

One reason for higher soil C and N concentrations at Lehavim may be higher inputs of C and N from plant litter at this site. Litterfall amounts and nutrient contents from our experiments are similar to those reported by other researchers for Chihuahuan Desert shrublands (Wilson and Thompson, 2005); we are not aware of other reports of litterfall collection in Negev Desert shrublands. During one year, C inputs from litterfall to soils of macrophytic patches were more than three times higher at Lehavim than at FHMR. The difference in N input was lower, because of the higher C:N ratio of litter at Lehavim (mean = 42, S.D. = 18, $n = 20$) compared to FHMR (mean = 19, S.D. = 4, $n = 20$). The higher soil C and N at Lehavim could also be partly due to differences in root biomass between the sites. Hibbard et al. (2001) reported that fine root biomass contributed more C and N to soil than did litterfall in a semi-arid grassland invaded by *Prosopis glandulosa*. However, we did not evaluate root biomass.

The difference in rainfall distribution may provide another explanation for differences in soil C and N between sites. Water is often the most limiting resource to biological activity in semi-arid lands (Noy-Meir, 1973). Soil respiration is driven by daily and seasonal temperatures, if moisture is not limiting. In the Mediterranean climate of the Negev, soil moisture is often not limiting during Winter, when soil temperatures are lowest. In the Chihuahuan Desert, approximately 50% of annual rainfall occurs during the warm Summer months. Thus, rapid rates of biological activity and OM mineralization may occur immediately following summer rainfall events. Xu et al. (2004) recently reported rapid respiration response in a California grassland to a small Summer rainfall event (12.5 mm) with near surface (2 cm depth) soil CO_2 concentrations increasing from 620 ppm (baseline) to 7100 ppm in <2 h. Steinberger and Whitford (1988) found that adding water to plant litter significantly increased rates of decomposition during summer in the Negev. Whitford et al. (1986) found that most decomposition occurred during the summer in a Chihuahuan ecosystem.

4.2. C and N isotopes

At Lehavim, most plant species use the C3 photosynthetic pathway. The C3 pathway results in a δ^{13}C of -27 ± 6‰ in plant tissue (Biggs et al., 2002). The δ^{13}C in litter within macrophytic patches at Lehavim was -25.9‰ (S.D. = 1.3, $n = 20$). The average soil δ^{13}C values of -15 to -18‰, and the relative absence of C4 species, suggest the presence of other, isotopically heavier, sources of C. Previous research has shown that microphytic patches within the northern Negev are dominated by cyanobacteria such as *Microcoleus vaginatus* and *Nostoc punctiforma* (Zaady et al., 1998). Cyanobacterial tissue possesses a δ^{13}C of -12‰ (Aranibar et al., 2003). Thus, the δ^{13}C values we report (Fig. 2(A)) suggest influence from cyanobacterial C, in both macrophytic and microphytic patches, with relatively more cyanobacterial C in soils of microphytic patches. These data appear to confirm the microphytic-macrophytic source–sink relationship within the patchy shrublands of the Negev, previously discussed by Zaady et al. (2001a). This, however, is the first C isotope evidence reported for this source–sink relationship.

The dominant C sources at FHMR are *Prosopis*, with an average litter δ^{13}C of -26.2‰ ($n = 20$, S.D. = 0.9), and C3 and C4 grasses. Biggs et al. (2002) reported that C4 grasses at FHMR had an average δ^{13}C of -14.3‰. Therefore, the values we report for the 0–5 cm depth (ca. -19.5‰, Fig. 2(A)) suggest considerable mixing of C3 and C4 C. While we found only 1‰ difference between macrophytic and microphytic patch soil C, this difference was significant ($p < 0.05$), and confirms greater C3 influence within macrophytic patches.

The average δ^{15}N of *Prosopis* litter was 0.9‰ (S.D. = 0.5, $n = 20$) and the δ^{15}N of litter collected in macrophytic patches at Lehavim (mostly *Sarcopoterium* litter) was 0.6‰ (S.D. = 2.0, $n = 20$). A δ^{15}N of 0 in theory indicates that all plant N is derived from N_2 fixation (Lopez Villagra and Felker, 1997; Robinson, 2001), therefore these δ^{15}N values suggest N_2 fixation as the primary source of plant N at both sites. However, a reliable estimate of the percentage of plant N from N_2 fixation requires knowledge of N source pools (Robinson, 2001), which were not available for either site. It is possible that these low δ^{15}N values could also result from uptake of NO_3^-, which often has a δ^{15}N lower than that of soil NH_4^+ (Falkengrun-Grerup et al., 2004). Nevertheless, other authors have reported higher δ^{15}N than these for leaves of *Prosopis* spp. (e.g. Geesing et al., 2000; Lopez-Villagra and Felker, 1997). Therefore, it is reasonable to assume that symbiotic N_2 fixation by *Prosopis* is a (or the) major contributor of N to this ecosystem. Zaady et al. (1998) suggested that as much as 40% of total N fixation within patchy Negev landscapes may occur by non-symbiotic fixation within macrophytic patches. Using the same reasoning as above, and the δ^{15}N of 0.6‰ of litter at this site, we suggest that virtually all N taken up by *Sarcopoterium* is derived directly from nonsymbiotic N fixation within the macrophytic patches, and N fixation by cyanobacteria and non-symbiotic microorganisms from nearby microphytic patches. This N may be transported to macrophytic patches by overland water runoff as discussed by Zaady et al. (2004). Russow et al. (2004) estimated that 46–86% of biomass N (δ^{15}N of 1–6‰) in the N-fixing shrub *Retama reatam* in the northern Negev was derived from N fixation. The δ^{15}N of SON (0–5 cm) was higher in microphytic patches at both sites (Fig. 2(B)). Evans and Ehleringer (1993) reported similar results for soils of Utah, USA, and attributed the higher δ^{15}N of microphytic patches to higher rates of N loss compared to macrophytic patches. Conversely, Billings et al. (2003) reported lower δ^{15}N in microphytic patches of Mohave Desert soils, along with higher rates of C_2H_2 reduction, thus indicating higher potential for N_2 fixation. Thus, our results are evidence of the importance of symbiotic N fixation within macrophytic patches for the N budget of these ecosystems.

4.3. Soil carbohydrates

Carbohydrate concentrations (0–5 cm) were not significantly different between the sites (Table 5). At both sites, about 10% of SOC was recovered as CHs, more than the 3% of SOC that Metting (1993) identified as typical, likely due to improved hydrolysis conditions with the analytical method we used (Martens and Loeffelmann, 2002). At

Lehavim, grazing resulted in lower soil CH, perhaps reflecting changes in short-term inputs. However, grazing did not significantly change SOC. The CH concentrations at both sites were higher than the 0.97–1.51 g/kg reported from shrub and grasslands in arid (210 mm rainfall) southern New Mexico by Gallardo and Schlesinger (1995). Similar to results reported by Martens et al. (2003) for Nebraska soils, the most common CH at both sites was glucose (Table 2).

4.4. Soil amino acids and sugars

Amino acids and sugars are the key substrates for production of inorganic N from mineralization (Metting, 1993), and AA and AS typically constitute a majority of soil N (Martens et al., 2003). A higher percentage of soil N was amino N at FHMR (60%, S.D. = 3.5) compared to Lehavim (49%, S.D. = 8.4). These percentages are consistent with results from soils from a wide variety of environments (Senwo and Tabatabai, 1998).

4.5. Asparaginase activity

L-asparaginase activity is related to N mineralization potential in soils (Dodor and Tabatabai, 2003). Asparaginase appears to have no activity outside of biological cells. Thus, its activity originates from living cells, intact dead cells, and cellular debris (Miller and Dick, 1995). The values at Lehavim are similar to those reported by Blank (2002) for asparaginase activity in arid soils of northern California (up to 66 μg N/g 2 h) and by Dodor and Tabatabai (2003) for cropped soils in Iowa (up to 97 μg N/g 2 h). Values at FHMR were one-third those at Lehavim, with no significant differences among patch types (Fig. 3(F)). At FHMR much of the enzyme activity was concentrated within O horizon material, where average asparaginase activity was 78.4 μg N/g 2 h ($n = 15$, S.D. = 54.6). However, the O horizon was dry most of the time, which will likely limit actual N mineralization. Asparaginase activity was not related to SOC at either site. The reasons for this are not clear; Blank (2002) reported significant correlations between SOC and asparaginase activity in desert soils in California, USA.

4.6. Available soil N and P

The combination of higher SON, higher CH, AA, and AS concentrations, and higher enzyme activity at Lehavim likely combined to result in higher concentrations of inorganic N throughout the year at Lehavim (Fig. 4(A)) compared to FHMR (Fig. 4(C)), for it is these factors that determine N mineralization potential. The inorganic N concentrations at Lehavim were higher than those normally reported for comparable arid and semi-arid environments, while those found at FHMR were more typical. For example, Gallardo and Schlesinger (1995) reported extractable N of 4 to 7.5 mg/kg within shrub and grasslands in arid southern New Mexico (210 mm annual rainfall). Cross and Schlesinger (1999) reported soil NO_3^- concentrations up to 13 mg/kg in semi-arid central New Mexico. Smith et al. (1994) found that average inorganic N was <4 mg/kg in a semi-arid shrubland in Washington state. During two years, Wilson and Thompson (2005) reported maximum mean soil inorganic N (0–10 cm) of <12 mg/kg at FHMR. Xie et al. (2001) reported maximum mean soil inorganic N (0–10 cm) of 16 mg/kg in the Judean Desert of Israel. Thus, the Lehavim site appears to have higher concentrations of SON, labile N (AA and AS N), and inorganic N than is typical for most arid and semi-arid soils.

Available soil P was much higher at FHMR (Fig. 4(D)) than at Lehavim (Fig. 4(B)), with an obvious "fertility island" effect at Lehavim, but not at FHMR. This difference in P distribution may result from the overall higher soil P status at FHMR. With such P concentrations, it would not be expected to limit plant growth. Considering the high available N at Lehavim, it is likely that P, rather than N, will limit plant growth, which will tend to promote P concentration within macrophytic patches (West and Klemmedson, 1978; Zaady et al., 1994).

4.7. Glucosamine:galactosamine ratios

Amino sugars appear to be unique to microorganisms, and are not present in higher plants. Glucosamine in soils is derived from fungal chitin as well as bacterial cell walls. Galactosamine, in contrast, results solely from bacteria and actinomycetes (Amelung et al., 2001). Thus, the ratio of glucosamine to galactosamine can be used to indicate the relative contribution of fungal-derived amino sugars to soil organic matter (Solomon et al., 2001). At Lehavim, the glucosamine:galactosamine ratio was significantly ($p<0.05$) affected by both grazing and patch type. The ratios were 2.42 and 2.49 within grazed and ungrazed macrophytic patches, respectively, and 2.58 and 2.78 in grazed and ungrazed microphytic patches. At FHMR, the glucosamine:galactosamine ratio was not different among patch types, and averaged 1.97. In a tropical soil, Solomon et al. (2001) found that after 15 yr of continuous cultivation, the glucosamine:galactosamine ratio increased from 1.44 to 2.23, suggesting that cultivation may have led to enrichment of fungal-derived amino sugars. Martens et al. (2003), reported glucosamine:galactosamine ratios of 1.47 and 1.94 in forested and cropped Nebraska soils, respectively. Our results from Lehavim suggest that fungi are more important cyclers of organic materials within microphytic than macrophytic patches. Differences between the sites suggest that fungi are proportionately more important at Lehavim than at FHMR.

4.8. Grazing effects at Lehavim

Grazing resulted in higher amounts of litterfall, probably due to effects of animals browsing on the shrubs. While there were no significant differences in SOC or SON with grazing (Table 1), grazing did result in lower soil concentrations of the most labile forms of C and N, viz. the CHs, AA, and AS (Figs. 3(A) and (B), Table 1). These reductions in resource input were accompanied by higher soil C:N with grazing, and lower concentrations of inorganic N. Caution should be exercised when interpreting and extrapolating these results; however they suggest that grazing may result in long-term reductions in soil C and N pools in this ecosystem due to reduced inputs of CH and amino forms of N. The implications of this could be long-reaching, and certainly deserve further study.

4.9. Structure of fertile islands

Our original prediction that more distinct differences in soil nutrient pools between patch types should exist in the more arid environment was supported by our results. Garner and Steinberger (1989) proposed that, under desert conditions, the biological processes that tend to concentrate C, N and P dominate over the physical processes that tend to disperse these nutrients. As relative ambient moisture increases, a transition point is reached at which the dispersive physical processes dominate over the concentrating biological processes. Thus, the fertile island effect should diminish along a continuum of increasing annual rainfall. In accord with the hypothesis presented by Garner and Steinberger (1989), differences between the sites can likely be attributed to the increasing importance of physical processes of resource dispersion at the more humid site in Arizona.

5. Conclusions

Within these semi-arid ecosystems, macrophytic patches are centers of C and N fixation through the influences of litterfall and N_2 fixation. Differences in soil C and N pools between patch types was more pronounced at the more arid Lehavim site, and soil (0–5 cm) OC, ON, AA, AS, asparaginase activity and inorganic N were all higher at Lehavim compared to FHMR. We conclude that differences between the two sites are due largely to (1) higher litterfall inputs in macrophytic patches at Lehavim and (2) different precipitation patterns, with Winter precipitation only at Lehavim and bimodal (Summer–Winter) precipitation at FHMR. Precipitation patterns impact mineralization rates of organic inputs and are important for regulating C and N cycling in these semiarid ecosystems. The result will likely be higher rates of OM mineralization at FHMR than at Lehavim, which helps to explain the much higher SOC and SON at Lehavim compared to FHMR.

In both ecosystems, disturbance involving removal (e.g. mechanical removal, burning) or disturbance (e.g. grazing) of the macrophytes would dramatically reduce C and N inputs into these soils. Livestock grazing was possible only at the Lehavim site—and resulted in lower concentrations of the most labile soil C (CH) and N pools (AA, AS, inorganic N). Changes in precipitation patterns induced by climate change could also change temporal patterns of mineralization of OM inputs, and consequently, change soil C and N pools. For example, a shift toward less summer precipitation in the Chihuahuan ecosystem, as predicted by some climate models (e.g. Smith et al., 2001) would likely reduce OM mineralization and increase soil C and N storage. Conversely, a shift toward summer precipitation in the Negev would likely increase rates of OM mineralization and decrease soil C and N.

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References

Amelung, W., Kimble, J.M., Samson-Liebig, S., Follett, R.F., 2001. Restoration of microbial residues in soils of the conservation reserve program. Soil Science Society of America Journal 65, 1704–1709.

Aranibar, J.N., Anderson, I.C., Ringrose, S., Macko, S.A., 2003. Importance of nitrogen fixation in soil crusts of southern African arid ecosystems: acetylene reduction and stable isotope studies. Journal of Arid Environments 54, 345–358.

Biggs, T.H., Quade, J., Webb, R.H., 2002. $\delta^{13}C$ values of soil organic matter in semiarid grassland with mesquite (*Prosopis*) encroachment in southeastern Arizona. Geoderma 110, 109–130.

Billings, S.A., Schaeffer, S.M., Evans, R.D., 2003. Nitrogen fixation by biological soil crusts and heterotrophic bacteria in an intact Mojave Desert ecosystem with elevated CO_2 and added soil carbon. Soil Biology and Biochemistry 35, 643–649.

Blank, R.R., 2002. Amidohydrolase activity, soil N status, and the invasive crucifer *Lepidium latifolium*. Plant and Soil 239, 155–163.

Brown, J.R., Archer, S., 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. glandulosa) on sites differing in herbaceous biomass and grazing history. Oecologia 80, 19–26.

Cross, A., Schlesinger, W., 1999. Plant regulation of soil nutrient distribution in the northern Chihuahuan Desert. Plant Ecology 145, 11–25.

Dodor, M.E., Tabatabai, M.A., 2003. Amidohydrolases in soils as affected by cropping systems. Applied Soil Ecology 24, 73–90.

Evans, R.D., Ehleringer, J.R., 1993. A break in the nitrogen cycle of aridlands: evidence from $\delta^{15}N$ of soils. Oecologia 94, 314–317.

Falkengrun-Grerup, U., Michelsen, A., Olsson, M.O., Quarmby, C., Sleep, D., 2004. Plant nitrate use in deciduous woodland: the relationship between leaf N, 15N natural abundance of forbs and soil N mineralisation. Soil Biology and Biochemistry 36, 1885–1891.

Gallardo, A., Schlesinger., W.H., 1995. Factors determining soil microbial biomass and nutrient immobilization in desert soils. Biogeochemistry 28, 55–68.

Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of 'Fertile Islands' in the desert ecosystem. Journal of Arid Environments 16, 257–262.

Geesing, D., Felker, P., Bingham, R.L., 2000. Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development:

implications for global carbon sequestration. Journal of Arid Environments 46, 157–180.

Gomez, K.A., Gomez, A.A., 1984. Statistical Procedures for Agricultural Research. Wiley, New York.

Harris, D., Horwath, W.R., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. Soil Science Society of America Journal 65, 1853–1856.

He, X., Mouratov, S., Steinberger, Y., 2002. Temporal and spatial dynamics of vesicular–arbuscular mycorrhizal fungi under the canopy of *Zygophyllum dumosum* Boiss in the Negev Desert. Journal of Arid Environments 52, 379–387.

Herman, R.P., Provencio, K.R., Herrara-Matos, J., Torrez, R.J., 1995. Resource islands predict the distribution of heterotrophic bacteria in Chihuahuan Desert soils. Applied and Environmental Microbiology 61, 1816–1821.

Hibbard, K.A., Archer, S., Schimel, D.S., Valentine, D.W., 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82, 1999–2011.

Keeney, D.R., Nelson, D.W., 1982. Nitrogen—inorganic forms. In: Page, A.L., et al. (Eds.), Methods of Soil Analysis, Part 2, second ed. Agronomy Monograph 9. ASA and SSSA, Madison, WI, pp. 672–673.

Kieft, T.L., White, C.S., Loftin, S.R., Aguilar, R., Craig, J.A., Skaar, D.A., 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. Ecology 79, 671–683.

Killingbeck, K.T., Whitford, W.G., 1996. High foliar nitrogen in desert shrubs: an important ecosystem trait or defective desert doctrine? Ecology 77, 1728–1737.

Kuo, S., 1996. Phosphorus. In: Sparks, D.L., et al. (Eds.), Methods of Soil Analysis, Part 3, Chemical Methods. SSSA Book Series No. 5. Soil Science Society of America, Madison, WI, pp. 869–919.

Lopez Villagra, G.M., Felker, P., 1997. Influence of understory removal, thinning and P fertilization on N_2 fixation in a mature mesquite (*Prosopis glandulosa* var. *glandulosa*) stand. Journal of Arid Environments 36, 591–610.

Martens, D.A., Loeffelmann, K., 2002. Improved accounting of carbohydrate carbon from plants and soils. Soil Biology and Biochemistry 34, 1393–1399.

Martens, D.A., Loeffelmann, K., 2003. Soil amino acid composition quantified by acid hydrolysis and anion chromatography—pulsed amperometry. Journal of Agricultural and Food Chemistry 51, 6521–6529.

Martens, D.A., Reedy, T.E., Lewis, D.T., 2003. Soil organic carbon content and composition of 130-year crop, pasture, and forest land-use managements. Global Change Biology 10, 65–78.

Metting Jr., F.B., 1993. Soil Microbial Ecology. Marcel Dekker, New York.

Miller, M., Dick, R.P., 1995. Thermal stability and activities of soil enzymes as influenced by crop rotations. Soil Biology and Biochemistry 27, 1161–1166.

Noy-Meir, E., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4, 23–51.

Osem, Y., Sternberg, M., Perevolotsky, A., Kigel, H., 1999. Species composition and abundance of annual plants in the seed bank and in the vegetation in a semiarid region in the northern Negev as affected by sheep grazing. Ecology and Environment 5, 180–189 (in Hebrew).

Perevolotsky, A., 1999. Natural conservation, reclamation, and livestock grazing in the northern Negev: contradictory or complementary concepts? In: Hoekstra, T.W., Shachak, M. (Eds.), Arid Lands Management; Toward Ecological Sustainability. University of Illinois Press, Urbana, pp. 223–232.

Polley, H.W., Johnson, H.B., Mayeux, H.S., 1994. Increasing CO_2: comparative responses of the C4 grass *Schizachyrium* and grassland invader *Prosopis*. Ecology 75, 976–988.

Robinson, D., 2001. $\delta^{15}N$ as an integrator of the nitrogen cycle. Trends in Ecology and Evolution 16, 153–162.

Russow, R., Veste, M., Littmann, T., 2004. Using the natural ^{15}N abundance to assess the main nitrogen inputs into the sand dune area of the North-western Negev Desert (Israel). Isotopes in Environment Health Studies 40, 57–67.

SAS Institute, 2000. The SAS System for Windows. Release 6.10. SAS Institute, Cary, NC.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. Science 247, 1043–1048.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E., Cross, A.F., 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Senwo, Z.N., Tabatabai, M.A., 1998. Amino acid composition of soil organic matter. Biology and Fertility of Soils 26, 235–242.

Shem-Tov, S., Zaady, E., Groffman, P., Gutterman, Y., 1999. Soil carbon content along rainfall gradient and germination: a potential mechanism for regulating of *Plantago coronopus*. Soil Biology and Biochemistry 31, 1209–1217.

Smith, J.L., Halvorson, J.J., Bolton Jr., H., 1994. Spatial relationships of soil microbial biomass and C and N mineralization in a semi-arid shrub-steppe ecosystem. Soil Biology and Biochemistry 26, 1151–1159.

Smith, J.B., Richels, R., Miller, B., 2001. Potential consequences of climate variability and change for the western United States. In: National Assessment Synthesis Team, U.S. Global Change Research Program, Climate Change Impacts on the United States. Cambridge University Press, Cambridge, UK, pp. 219–245.

Solomon, D., Lehmann, J., Zech, W., 2001. Land use effects on amino sugar signature of chromic Luvisol in the semi-arid part of northern Tanzania. Biology and Fertility of Soils 33, 33–40.

Steinberger, Y., Whitford, W.G., 1988. Decomposition process in Negev ecosystems. Oecologia 75, 61–66.

Tabatabai, M.A., 1994. Soil enzymes. In: Weaver, R.W., et al. (Eds.), Methods of Soil Analysis. Part 2: Microbiological and Biochemical Properties. Soil Science Society of America, Madison, WI, pp. 775–833.

Tiedemann, A.R., Klemmedson, J.O., 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. Journal of Range Management 30, 361–367.

Tiedemann, A.R., Klemmedson, J.O., 1986. Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. Soil Science Society of America Journal 50, 472–475.

Ungar, H.D., Perevolotsky, A., Yonatan, R., Barkai, D., Hefetz, Y., Baram, H., 1999. Primary production of natural pastures of the hilly northern Negev—contributory factors and management implications. Ecology and Environment 5, 130–138 (in Hebrew—abstract in English).

West, N.E., Klemmedson, J.O., 1978. Structural distribution of nitrogen in desert ecosystems. In: West, N.E., Skujins, J.J. (Eds.), IBP Synthesis Series 9. Dowden, Hutchinson, and Ross, Inc., Pennsylvania, pp. 1–16.

Western Regional Climate Center, 2005. 1971–2000 monthly climate summary for Fort Huachuca, Arizona. http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?azfthu (accessed, 23.03.2005).

Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, San Diego, CA.

Whitford, W.G., Steinberger, Y., MacKay, W., Parker, L.W., Freckman, D., Wallwork, J.A., Weems, D., 1986. Rainfall and decomposition in the Chihuahuan Desert. Oecologia 68, 516–520.

Wilson, T.B., Thompson, T.L., 2005. Soil nutrient distributions of mesquite-dominated desert grasslands: changes in time and space. Geoderma 126, 301–315.

Wilson, T.B., Webb, R.H., Thompson, T.L., 2001. Mechanisms of range expansion and removal of mesquite in desert grasslands in the southwestern United States. Gen. Tech. Rep. RMRS-GTR-81. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT, 23pp.

Xie, G., Lahav, I., Barness, G., Steinberger, Y., 2001. Dynamics of soil nitrogen along a topoclimatic gradient in the Judean Desert. Arid Land Research and Management 15, 135–146.

Xu, L., Baldocchi, D.D., Tang, J., 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. Global Biogeochemical Cycles 18, GB4002.

Zaady, E., Okon, Y., Perevolotsky, A., 1994. Growth response of Mediterranean herbaceous swards to inoculation with *Azospirillum brasilense*. Journal of Range Management 47, 12–15.

Zaady, E., Groffman, P.M., Shachak, M., 1996. Litter as a regulator of N and C dynamics as macrophytic patches in Negev Desert soils. Soil Biology and Biochemistry 28, 39–46.

Zaady, E., Groffman, P., Shachak, M., 1998. Nitrogen fixation in macro- and microphytic patches in the Negev Desert. Soil Biology and Biochemistry 30, 449–454.

Zaady, E., Shachak, M., Moshe, Y., 2001a. Ecological approach for afforestation in arid regions of the northern Negev Desert, Israel. In: Vajpeyi, D.K. (Ed.), Deforestation, Environment, and Sustainable Development. Praeger, Westport, CT, pp. 219–238.

Zaady, E., Yonatan, R., Shachak, M., Perevolotsky, A., 2001b. The effects of grazing on abiotic and biotic parameters in a semiarid ecosystem: a case study from the northern Negev Desert, Israel. Arid Land Research and Management 15, 245–261.

Zaady, E., Levacov, R., Shachak, M., 2004. Application of the herbicide, Simazine, and its effect on soil surface parameters and vegetation in a patchy desert landscape. Arid Land Research and Management 18, 397–410.